

The influence of external subsidies on diet, growth and Hg concentrations of freshwater sport fish: implications for management and fish consumption advisories

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Abstract Mercury (Hg) contamination in sport fish is a global problem. In freshwater systems, food web structure, sport fish sex, size, diet and growth rates influence Hg bioaccumulation. Fish stocking is a common management practice worldwide that can introduce external energy and contaminants into freshwater systems. Thus, stocking can alter many of the factors that influence Hg concentrations in sport fish. Here we evaluated the influence of external subsidies, in the form of hatchery-raised rainbow trout *Oncorhynchus mykiss* on walleye *Sander vitreus* diet, growth and Hg concentrations in two freshwater systems. Stocking differentially influenced male and female walleye diets and growth, producing a counterintuitive size-contamination relationship. Modeling indicated that walleye growth rate and diet were important explanatory variables when predicting Hg concentrations. Thus, hatchery contributions to freshwater systems in the form of energy and contaminants can influence diet, growth and Hg concentrations in sport fish. Given the extensive scale of fish stocking, and the known health risks associated with Hg contamination, this represents a significant issue for

managers monitoring and manipulating freshwater food web structures, and policy makers attempting to develop fish consumption advisories to protect human health in stocked systems.

Keywords Bioaccumulation · Walleye · Hatchery subsidies · Rainbow trout · Stocking

Introduction

Mercury (Hg) is one of the most important contaminants in fish because it is ubiquitous and significantly impacts the health of humans and ecosystems worldwide (Driscoll et al. 2007; Mergler et al. 2007). Consumption of Hg contaminated fish is the primary transfer pathway of aquatic Hg to humans; however, the health benefits of eating fish may offset risks associated with Hg contamination (Knuth et al. 2003; Mergler et al. 2007). Thus, it is essential to understand the mechanisms of Hg bioaccumulation in fish to minimize the risks associated with fish consumption while maintaining the nutritional benefits.

The influence of a variety of factors on Hg concentrations in fish has been evaluated. For example, fish sex (Henderson et al. 2003; Rennie et al. 2008), size (Harris and Bodaly 1998), diet and trophic position (Harris and Bodaly 1998; Power et al. 2002; Sackett et al. 2010) and growth (Simoneau et al. 2005; Ward et al. 2010) have all been shown to play a role in Hg bioaccumulation. Anthropogenic manipulation of food webs can alter the dynamics of these factors. For example, fish stocking, a common practice in fisheries management, can influence fish density, growth, size and age structure and community structure (Cowx 1997; Kohler and Hubert 1999). Theoretical work has shown the potential of stocking as a means

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to reduce contaminant concentrations in sport fish by promoting high growth rates, which in turn, dilute contaminants (Stow et al. 1995). This mechanism, known as growth dilution, occurs when, *ceteris paribus*, fish that accumulate somatic tissue more efficiently and achieve larger sizes more quickly have lower contaminant concentrations than smaller, less efficient, slower-growing individuals (Verta 1990; Ward et al. 2010). Growth dilution has been observed in sport fish, where females of the species grew more efficiently and had lower Hg concentrations relative to males with similar diets (Rennie et al. 2008). Similarly, biomass dilution occurs in individual or populations of sport fish when, *ceteris paribus* (e.g., prey Hg concentration, availability, etc.) prey species of relatively high quality (high energy content) are consumed rather than prey species of lower quality (low energy content), resulting in decreased Hg concentration (Lepak et al. 2012). Stocking relatively high quality (high energy content), low Hg prey for sport fish consumption has the potential to simultaneously induce biomass dilution and reduce overall Hg intake by sport fish, potentially causing greater reductions in Hg concentrations than achievable by either process alone.

The magnitude of fish stocking in fisheries management is enormous: approximately 2 billion fish are stocked annually around the world, excluding private hatchery production (Halverson 2010). Hatchery-reared rainbow trout (*Oncorhynchus mykiss*; RBT) for example, have been distributed in every state in the United States, at least 80 countries worldwide and every continent except Antarctica (Halverson 2010). Rainbow trout production has increased in recent years and Europe, North America, Chile, Japan and Australia are among the primary producers (FAO 2009). Rainbow trout and other salmonid species are often stocked to create angling opportunities, but may become prey for larger, apex predators (Flinders and Bonar 2008; Marwitz and Hubert 1997; Yule et al. 2000). As a result, these predators can experience increased growth rates (Beyerle 1971; Johnson and Martinez 2000) and relative weights (W_r), indicating better condition (Flinders and Bonar 2008; Marwitz and Hubert 1997). Over 20 countries maintain stocking programs for sport fish on six continents with prominent operations in Africa, Australia, Europe, North America and South America (Crawford and Muir 2008). Thus, stocking may be having impacts on fish growth and Hg concentrations at much larger scales than previously considered.

Mercury is transferred to humans through primary, secondary and, as we examine here, tertiary pathways. Fish consumption represents the primary pathway of Hg to humans (Mergler et al. 2007). Secondarily, the transport of pollutants to humans also occurs through consumption of beef, dairy products, poultry, eggs and pork when external

energy (e.g., marine or freshwater-derived fish meal) is used to feed farm animals (Dórea 2006; Lindberg et al. 2004) and this is largely overlooked (Dórea 2009) despite the rapid increase in production and use of fish meal in hatchery, aquaculture and agriculture operations. For example, currently, 20–30 million metric tons of fish are used annually to produce fish meal, of which, 60 % is used in aquaculture and hatchery operations (FAO 2009). Tertiary Hg exposure to humans (an even more obscure pathway) may occur through the consumption of sport fish that have consumed cultured fish that are stocked. In this case, stocked fish may represent a less contaminated or more contaminated source of prey for sport fish, depending on relative Hg concentrations found in stocked and naturally available prey.

We evaluated the influence of fish stocking on sport fish growth and Hg concentrations because: (1) fish stocking is a ubiquitous practice, (2) stocking can contribute to sport fish growth which may dilute Hg concentrations and (3) stocking can be an external source of Hg to freshwater systems in the form of stocked fish. Specifically, we examined the contribution of external energy and contaminants in the form of hatchery-raised RBT, to diet, growth and Hg concentrations of walleye (*Sander vitreus*). Walleye have a widespread distribution and are very popular in North America as a sport fish targeted for harvest and consumption by anglers and their families (Quinn 1992). We selected two freshwater reservoirs, Carter and Brush Hollow reservoirs (Colorado, USA) as study systems. The reservoirs are typical of many reservoirs, with highly managed fisheries and water content serving agricultural, municipal and recreational demands.

Methods and materials

Site descriptions

Carter Reservoir (CR) (Larimer County, CO, USA, 40°20'N, 105°13'W) is a 453 ha impoundment created in 1952 with a capacity of approximately 138 million m³ and maximum depth of approximately 55 m. Brush Hollow Reservoir (BHR) (Fremont County, CO, USA, 38°27'N, 105°03'W) is a 75 ha impoundment created in 1907 with a capacity of approximately 5 million m³ and maximum depth of approximately 14 m. Both reservoirs receive water from outside of the watersheds in which they are contained through pumping operations. Each reservoir receives water in variable amounts from multiple sources outside of their watersheds depending on the daily, seasonal, and annual availability of external water sources. Chemical and morphological attributes of the study reservoirs are provided in Table 1.

Table 1 Reservoir characteristics

Attribute	Brush Hollow Reservoir	Carter Reservoir
Secchi depth (m) \pm SD (<i>N</i>)	2.16 \pm 1.86 (5)	2.76 \pm 1.43 (21)
Total phosphorus (mg/L) \pm SD (<i>N</i>)	0.03 \pm 0.02 (5)	0.01 \pm 0.01 (25)
Total nitrogen (mg/L) \pm SD (<i>N</i>)	0.23 (1)	0.21 \pm 0.05 (4)P
Primary substrate in watershed	Shale and limestone	Mudstone and sandstone
Δ Depth May–September in m (year)	–1.4 (2009)	–2.4 (2008)
Surface area (ha)	75	453
Elevation (m)	1673	1757

Available surface water quality attributes were measured from 2000—present by Colorado Parks and Wildlife personnel. Only those data from June to August are included. Watershed substrates were obtained from the United States Geological Survey. Change in water level from May to September was monitored during the sampling periods in each reservoir respectively. Reservoir area and elevation were obtained by Colorado Parks and Wildlife personnel

The study reservoirs are managed as two-tiered fisheries with walleye and RBT representing the two tiers. Historically, CR and BHR have been stocked with approximately 9,000 and 3,000 kg of RBT (respectively) annually, with stocking spread systematically (\sim monthly) throughout the open-water period to replace RBT lost from previous stocking events. Few rainbow trout are observed during subsequent sampling surveys and individual walleye exceeding 5 and 4 kg in CR and BHR respectively have been consistently sampled within these systems (Colorado Parks and Wildlife, pers. comm.).

Organism collections

Walleye were collected from CR with gillnets on 27 October 2008. Relatively small (48–92 mm) prey fish were collected using a combination of bag seines and electrofishing throughout August 2008. Crayfish (*Orconectes* spp; 83–116 mm) were collected during three sampling periods: June, July and September 2008 using commercially available crayfish traps. Rainbow trout (120–263 mm) were collected directly from a Colorado hatchery facility on 26 August 2008.

Walleye were collected from BHR with gillnets on 16 October 2009. A variety of prey fish at sizes available for walleye consumption were collected by electrofishing on 3 June and 5 August 2009. Relatively small crayfish (22–96 mm) were collected during three sampling periods: July, August and October 2009 by a combination of snorkeling and commercially available crayfish traps. All individuals from CR and BHR were weighed, measured, frozen and stored at -20°C until prepared for further analyses.

Mercury analyses

Muscle tissue from fish and crayfish was analyzed for Hg concentration. Individual walleye and aggregate prey fish samples were tested for total Hg (T-Hg) as a surrogate for

methylmercury (MeHg, the form of Hg that bioaccumulates and has toxic properties) assuming T-Hg was composed of 95 % or more MeHg (Bloom 1992). Muscle tissue from individual prey fish of similar lengths were aggregated ($n = 2-5$) by species and tested for T-Hg with the exception of one RBT sample containing a single individual tested for T-Hg. Crayfish were divided into two groups (small and large) by sample period and individuals ($n = 2-5$) in these size classes were aggregated for MeHg analysis. Means of crayfish total lengths and MeHg concentrations were aggregated and averaged across sample periods to develop a single metric of these characteristics representing the two size groups of crayfish.

All fish samples were analyzed on a wet weight basis. Crayfish were tested on a dry weight basis to facilitate MeHg analysis. Crayfish muscle tissue was dried for ≥ 72 h at 60°C and homogenized prior to MeHg analysis. Conversions of crayfish MeHg concentrations from a dry to wet basis were performed using mean wet weight percentages (75 %, $n = 33$; J.M. Lepak, unpublished data).

Reference materials of known Hg concentrations were used as quality controls including BCR 463 (tuna fish) and DOLT-3 (dogfish liver tissue). Samples tested for T-Hg were analyzed with a NIC MA-2000 (Nippon Instrument Corporation, Osaka, Japan) by combustion (EPA Method 7473). Percent recoveries of reference materials (BCR 463; $n = 27$ and DOLT-3; $n = 23$) for T-Hg ranged from 88.0 to 107.8 % with a mean of 98.3 ± 4.4 %. Samples tested for MeHg were analyzed using an ion chromatographic separation of cationic Hg-thiourea complexes, followed by sequential oxidation of CH_3Hg^+ to Hg^{II} , stannous chloride reduction of Hg^{II} to Hg^0 , evaporation of Hg^0 into an Ar carrier, drying of the sample gas, and finally atomic fluorescence detection. For further details about this method see Shade (2008). Percent recoveries of reference materials for MeHg (BCR 463; $n = 6$, DOLT-3; $n = 7$) ranged from 90.3 to 107.8 % with a mean of 100.2 ± 5.1 %. Percent recoveries of reference materials for inorganic Hg (BCR

463; $n = 6$, DOLT-3; $n = 7$; SRM 2976; $n = 1$) ranged from 100.0 to 107.8 % with a mean of 103.6 ± 2.5 %.

Stable isotope analyses

Samples tested for Hg concentrations were also tested for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ to estimate walleye diet composition. A sub-sample of each homogenized aggregate (prey fish and crayfish) or individual (walleye) sample was dried ≥ 72 h at 60°C prior to analysis. Means of crayfish total length and stable isotope signatures were pooled and averaged across sample periods to develop a single metric of these characteristics representing the two size groups of crayfish. Stable isotope analyses were performed using a Carlo Erba NC2500 elemental analyzer interfaced to a Thermo Finnigan MAT Delta Plus.

Standards used for normalization correction for CR and hatchery RBT samples were brown trout ($n = 16$, $\delta^{13}\text{C} = -25.59$ ‰, $\delta^{15}\text{N} = 17.43$ ‰, 49.53 % C, 13.90 % N) and corn ($n = 14$, $\delta^{13}\text{C} = -11.65$ ‰, $\delta^{15}\text{N} = 1.19$ ‰, 44.86 % C, 2.24 % N). Standards used to determine isotopic precision for CR samples were mink ($n = 32$, $\delta^{13}\text{C} = -25.21$ ‰, $\delta^{15}\text{N} = 10.47$ ‰, 49.70 % C, 13.50 % N) and rice ($n = 4$, $\delta^{13}\text{C} = -29.01$ ‰, $\delta^{15}\text{N} = 1.30$ ‰, 39.41 % C, 4.54 % N). A methionine standard ($n = 12$, $\delta^{13}\text{C} = -25.13$ ‰, $\delta^{15}\text{N} = -0.86$ ‰, 40.47 % C, 10.14 % N) was used to determine instrument linearity during the analysis of CR samples. The standard error from the mean of each standard material never exceeded 0.1 ‰ (range 0.01–0.09 ‰) during the isotopic run to determine sample $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures.

Standards used for normalization correction for BHR samples were brown trout ($n = 6$, $\delta^{13}\text{C} = -25.65$ ‰, $\delta^{15}\text{N} = 17.34$ ‰, 49.10 % C, 12.96 % N) and corn ($n = 6$, $\delta^{13}\text{C} = -11.82$ ‰, $\delta^{15}\text{N} = 1.09$ ‰, 45.01 % C, 2.12 % N). Standards used to determine isotopic precision for BHR samples were mink ($n = 8$, $\delta^{13}\text{C} = -25.27$ ‰, $\delta^{15}\text{N} = 11.32$ ‰) and rice ($n = 2$, $\delta^{13}\text{C} = -25.06$ ‰, $\delta^{15}\text{N} = -1.14$ ‰). A methionine standard ($n = 6$, $\delta^{13}\text{C} = -25.08$ ‰, $\delta^{15}\text{N} = -1.02$ ‰, 39.89 % C, 9.43 % N) was used to determine instrument linearity during the testing of BHR samples. The standard error from the mean of each standard material never exceeded 0.1 ‰ (range 0.01–0.09 ‰) during the isotopic run to determine sample $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures.

Samples that vary widely from a C:N ratio of 3.3 may require adjustments in $\delta^{13}\text{C}$ to account for lipid content if lipid extractions are not performed (Post et al. 2007). However, normalization and correction models for error associated with $\delta^{13}\text{C}$ signatures of non-lipid extracted tissues can produce biased estimates of fish tissue $\delta^{13}\text{C}$ (Mintenbeck et al. 2008). In this study, lipid extractions were not performed and walleye prey species and individual walleye C:N ratios ranged from 2.9 to 7.7

(mean \pm S.D. = 3.3 ± 0.6). All sample C:N ratios were ≤ 5.0 with two exceptions (5.2 and 7.7 for aggregate crayfish samples) and only five samples exceeded a C:N ratio of 4.0. Thus, it was assumed that differential fractionation did not influence the results presented here.

Energy density analyses

All aggregate prey fish samples collected from CR and the hatchery facility were analyzed for energy density. Aggregate samples of crayfish (small and large separately) collected in July from CR were also analyzed for energy density. Literature values were used as a proxy for prey energy density when measurements were unavailable.

Whole organisms were ground using liquid N_2 to produce a fine powder. A sub-sample of this powder was dried ≥ 72 h at 60°C . Samples were then compressed into pellets and burned in a Parr 1261 bomb calorimeter. Duplicate samples ($n = 2$) had differences of 0.8 and 1.7 % from the original values with a mean difference of 1.3 %.

Energy densities (dry weight) were converted to a wet weight basis for comparison with literature values assuming water content of 75 % for all prey fish (Hartman and Brandt 1995). Conversions of crayfish energy densities from a dry to wet basis were performed using mean wet weight percentages (75 %, $n = 33$; J.M. Lepak, unpublished data).

Walleye aging

Individual walleye ages were interpreted from sagittal otolith thin sections magnified at 32–160 \times . Checks in otoliths presumed to be annuli were used to assign ages to fish of known lengths by two independent readers and discrepancies in age assignments were resolved by a third independent reader.

Statistical analyses

We used a three component approach to evaluate relationships between walleye sex, weight, diet, growth and Hg concentration (Fig. 1). Essentially all of the covariates in this study were correlated and not directly causal. Thus, we modeled each of the three components individually, rather than using a larger predictive model with walleye Hg concentration as the response. By partitioning the model based on strong a priori understanding of the systems (e.g., sex may influence diet but diet cannot influence sex) we were able to include collinear variables and make inferences about the various model components. The general outline of our analysis can be described in a series of three steps: (1) Diet: compute an index of diet based on isotopic information for walleye and their potential food items and use this index as a response variable in a model with sex

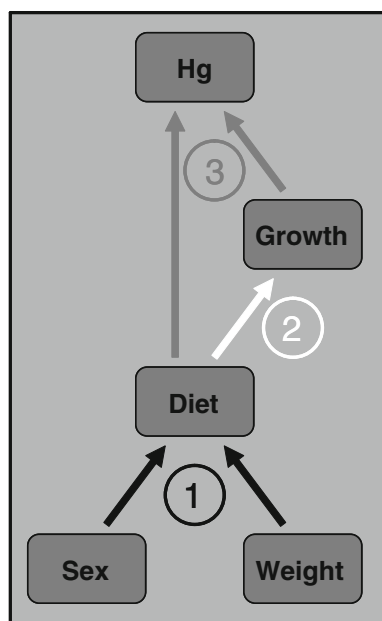


Fig. 1 Model describing components 1–3 of statistical analysis: (1) walleye diet as explained by sex and weight, (2) walleye growth as explained by walleye diet and (3) walleye Hg concentrations as explained by diet and growth. The colour of the arrows depicting each model component, correspond to the colour of the component numbered 1–3

and weight as covariates, (2) Growth: compute an index of walleye growth based on walleye age and weight and assess the effect of diet on walleye growth and (3) Hg: model walleye Hg concentration as a function of both growth and diet to assess their contribution to Hg bioaccumulation.

To assess the influence of sex and weight on walleye diet (component 1; Fig. 1), we quantified walleye diet using a bivariate mixture model that “paired” walleye with their potential prey based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures using 0.5 and 3.5 ‰ for trophic fractionation, respectively (France 1995; Vander Zanden and Rasmussen 2001). In this model we estimated p_i or the proportion of the diet of walleye i that was comprised of RBT versus all other prey items (denoted as “in-lake”) using mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of prey items to characterize their isotopic values.

After walleye diets were quantified it was possible to evaluate the influence of sex and weight on this response. Importantly, values of p_i exist on compact support (i.e., the interval 0–1) and could include both endpoints (zero and one). The latter caveat made standard transformation for use in linear regression difficult. Moreover, the covariates we used to describe walleye diet (sex and weight) were highly collinear and could potentially imply a heteroskedastic response, neither of which is easily dealt with using a conventional regression framework. Therefore, we applied a “beta regression” approach (e.g., Simas et al. 2010). In beta

regression the response is bounded by zero and one and can be explained in terms of two sets of covariates, one set for the mean and the other for the precision (inverse of variance). Here we specify $p_i \sim \text{Beta}(a_i, b_i)$ for $i = 1, \dots, n$, where we reparameterize the distribution such that $p_i \sim \text{Beta}(\mu_i, \varphi_i)$, for $\mu_i = a_i/(a_i + b_i)$ and $\varphi_i = a_i + b_i$. Then suitable transformations can be used to link the parameters μ_i and φ_i to sets of covariates. For example,

$$\Phi^{-1}(\mu_i) = \mathbf{x}'_i \boldsymbol{\beta}$$

$$\log(\varphi_i) = \mathbf{w}'_i \boldsymbol{\alpha}$$

where the symbol Φ^{-1} is referred to as the “probit” transformation (i.e., standard normal cumulative distribution function) and \mathbf{x}_i and \mathbf{w}_i denote the sets of covariates for observation i . The coefficients $\boldsymbol{\beta}$ and $\boldsymbol{\alpha}$ could then be thought of as regression parameters controlling the mean and precision of the likelihood, respectively. A major advantage of this approach was that it allowed us to use both covariates (sex and weight) in the same model despite their collinearity. Given that sex was a binary variable and we saw more diet dispersion in females than males, we used the sex variable as a covariate in the dispersion portion of the model and used weight as the covariate for the mean portion of the model.

Walleye sex was unknown for fish from CR. The Bayesian approach to the beta regression allowed us to statistically impute the unknown sex of walleye from CR so it could be used as a covariate for the precision portion of the beta regression. By giving CR walleye sex a prior distribution (i.e., Bernoulli with probability 0.5, where sex is designated as zero or one with one being female), we could sample from their full-conditional distribution while fitting the rest of the model using a Markov Chain Monte Carlo (MCMC) algorithm. This method referred to as “data augmentation” (Tanner and Wong 1987) provided a rigorous means to account for uncertainty in CR walleye sex. Using exchangeable normal priors for the beta regression coefficients (i.e., $\boldsymbol{\beta}$ and $\boldsymbol{\alpha}$) with mean zero and variance 100, we obtained 10,000 MCMC samples from the posterior distribution, discarding the first 1,000 as burn-in. Convergence was nearly immediate and Markov chains were very well mixed.

To assess the effect of walleye diet on growth (component 2; Fig. 1), we determined whether growth differed among fish consuming in-lake prey items versus those consuming RBT. To differentiate between these groups, we used a K-means cluster analysis on walleye $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures using three groups for each system. We then categorized two distinct groups as “in-lake” and “RBT” walleye (with a third group termed “unclassified” that did not fit in either group) in terms of general diet. Finally, we used nonlinear least squares to fit von Bertalanffy growth

functions (see equation below) to each cluster, combining lakes.

$$W_t = W_\infty (1 - \exp(-K(t - t_0)))^3 \quad (1)$$

where W_t is the weight at time t , W_∞ is the mean asymptotic weight, K is the Brody growth coefficient and t_0 is the hypothetical age at which the fish would have been 0 grams in weight (Ricker 1975). Confidence intervals were then used to determine if growth differences existed between the clusters of walleye.

To assess the effect of diet and growth on walleye Hg concentrations (component 3; Fig. 1), we characterized specific growth rates g using the exponential growth function:

$$g = [\log(w(\text{age})) - \log(w(\text{hatch}))] / \text{age} \quad (2)$$

where, $w(\text{age})$ and $w(\text{hatch})$ represented weight in grams at capture age and hatch (0.005 g; Siegwarth and Summerfelt 1993) respectively. We then used the full model:

$$\text{Hg}_i = \beta_0 + \beta_1 \log(g)_i + \beta_2 p_i + \varepsilon_i \quad (3)$$

where, the response Hg represented measured Hg concentrations in each fish and the covariates were as defined previously. Based on preliminary analysis, we found that $\log(g)$ and p_i were moderately correlated. Thus, we first evaluated the effect of multicollinearity on estimator variance by computing the variance inflation factors (VIF; e.g., O'Brien 2007) and also examined the change in estimated effects using a form of penalized regression called "ridge regression" (Hoerl and Kennard 1970). Ridge regression uses a penalty parameter to "shrink" the parameter estimates toward zero, thereby reducing any bias caused by the correlation between covariates. If the parameters estimated by ridge regression change little from the non-penalized regression then we can assume the effect of multicollinearity on the estimates is minimal.

Results

In all cases, in-lake prey sources had higher Hg concentrations and lower energy densities relative to RBT prey (see Table 2). The mixture model for component 1 (Fig. 1), demonstrated that CR walleye consumed either rainbow trout or in-lake prey sources almost exclusively, with few fish having a mixed diet (Fig. 2; also depicting the cluster analysis described below). In BHR, isotopic signatures indicated that walleye had a more complex diet, consuming a mixture of RBT and in-lake prey items (Fig. 2; also depicting the cluster analysis described below). In general, empirical walleye Hg concentrations increased consistently with weight up to approximately 1,000 g in each study

system, at which point Hg concentrations increased in variability (CR) and/or were lower than Hg concentrations of walleye weighing 1,000 g (CR and BHR; Fig. 3).

The model fitting walleye weight and sex as influences on walleye diet from component 1 (Fig. 1), showed that both parameters pertaining to the mean relationship between weight and diet were highly significant as indicated by the posterior 95 % credible intervals that do not overlap zero (Fig. 4). The parameters pertaining to precision corresponded to the effect of walleye sex on diet. Male walleye had significantly increased precision of the response variable (diet: proportion of RBT) beyond that of female walleye (i.e., reduced variance; Fig. 4). This supported the results from the mixture model that indicated female walleye had more variable diets than male walleye, with males focusing on in-lake prey items and females consuming in-lake prey items as well as RBT. The combined influence of walleye sex and weight on diet is best illustrated by viewing the posterior predictive distribution of the proportion of RBT in walleye diets versus weight (Fig. 4). From this it is clear that male walleye had a consistently low proportion of RBT in their diets, the proportion of RBT in walleye diets increased with increasing weight and the variability in walleye diet (due to increased RBT consumption) increases dramatically when walleye were female.

The combined results from the cluster analysis and subsequent fitting of the von Bertalanffy growth functions for component 2 (Fig. 1), indicated that walleye categorized as "in-lake" consumers grew poorly (i.e., reaching a lower mean asymptotic weight; W_∞) relative to walleye categorized as "RBT" consumers (Figs. 2, 5). Confidence intervals around the estimates of K were (0.324, 0.901) for walleye classified as "in-lake" consumers, and (0.237, 0.617) for walleye classified as "RBT" consumers. Note, the confidence intervals for W_∞ for "in-lake" (680, 1193) and "RBT" (3281, 4115) walleye did not overlap, suggesting that growth for the two clusters of walleye was indeed different.

For component 3 (Fig. 1), walleye diet (proportion of RBT; p_i) and walleye growth ($\log(g)$) were used in predictive models of walleye Hg concentrations. We found that the covariates were correlated, thus, we assessed the potential for multicollinearity to be influencing statistical inference by: (1) computing the variance inflation factors (VIFs) and (2) performing a ridge regression. The mean VIF was 1.78, which indicated only a slight effect due to multicollinearity (VIF < 5 as recommended in the literature; e.g., O'Brien 2007). Full model ridge regression coefficient estimates varied little from the non-penalized linear model (i.e., regression coefficients = (-0.181, -0.053), ridge regression coefficients = (-0.178, -0.051)) also indicating that the effect of multicollinearity

Table 2 Prey isotopic signatures, mercury concentrations and energy densities

Species (size)	Mean length (mm)	<i>n</i>	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	MeHg or T-Hg (mg/kg)	Energy density (J/g wet mass)
Carter Reservoir						
WHS	57	5	-20.3	8.2	0.021	3,382
WHS	69	5	-19.2	7.9	0.066	3,811
YPE	50	5	-27.1	9.5	0.022	4,662
YPE	62	5	-25.3	9.2	0.021	4,068
CFI (S)	92	8	-24.1	9.7	0.106	3,204 ^a
CFI (L)	110	8	-24.2	10.8	0.043	2,783 ^a
Brush Hollow Reservoir						
BCR	102	3	-21.8	9.7	0.060	4,186 ^b
BCR	184	2	-24.6	11.3	0.080	4,186 ^b
BGL	93	5	-23.2	10.3	0.029	4,186 ^c
BGL	113	5	-23.9	10.8	0.033	4,186 ^c
SNF	59	3	-21.4	10.3	0.039	4,186 ^c
SNF	110	4	-21.3	7.8	0.068	4,186 ^c
YPE	65	5	-18.8	7.9	0.049	4,186 ^c
YPE	140	3	-19.8	8.4	0.060	4,186 ^c
CFI (S)	39	15	-19.7	6.0	0.047	3,088 ^{d,e,f}
CFI (L)	70	14	-21.3	7.4	0.043	3,088 ^{d,e,f}
Hatchery						
RBT	126	4	-19.2	11.3	0.017	5,556
RBT	176	3	-20.3	10.7	0.017	5,624
RBT	211	2	-19.9	11.1	0.016	5,690
RBT	263	1	-20.3	11.1	0.014	5,937

All fish were tested for T-Hg and crayfish were tested for MeHg

BCR black crappie (*Pomoxis nigromaculatus*), BGL bluegill sunfish (*Lepomis macrochirus*), CFI(L) large crayfish (*Orconectes spp*), CFI(S) small crayfish, RBT rainbow trout (*Oncorhynchus mykiss*), SNF sunfish hybrids (*Lepomis spp*), WHS white sucker (*Catostomus commersonii*), YPE yellow perch (*Perca flavescens*)

^a Aggregate samples from July were tested to obtain values

^b Flinders and Bonar (2008)

^c Hanson et al. (1997)

^d King and Ball (1967)

^e Kelso (1973)

^f Probst et al. (1984)

was minimal. Thus, we continued with standard regression analysis, computing AIC weights for each of the submodels. The model carrying the most weight included both walleye growth and diet as covariates ($\Delta\text{AIC} = 0$, weight = 0.97), followed by the model with walleye growth as the only covariate ($\Delta\text{AIC} = 7.3$, weight = 0.03), with the other two models (diet only and null model) carrying the least weight in the model set ($\Delta\text{AIC} = 62.4$, weight <0.01 and $\Delta\text{AIC} = 69.2$, weight <0.01, respectively). These results indicated that both walleye growth (incorporating age and weight) and walleye diet (proportion RBT) were important explanatory variables when modeling Hg concentrations.

Discussion

The results presented here have widespread implications with respect to fisheries management and human health, given the extensive use of stocked fish in freshwater systems and the fact that fish Hg advisories are usually length-based. Hatchery subsidies had significant effects on sport fish populations in two freshwater systems by altering: (1) sport fish diet, (2) sport fish growth and (3) sport fish Hg concentrations. Large walleye (~5 kg) consuming RBT (relatively high in energy density and low in Hg concentration) had Hg concentrations lower than some smaller walleye (~1 kg) consuming in-lake prey items. In

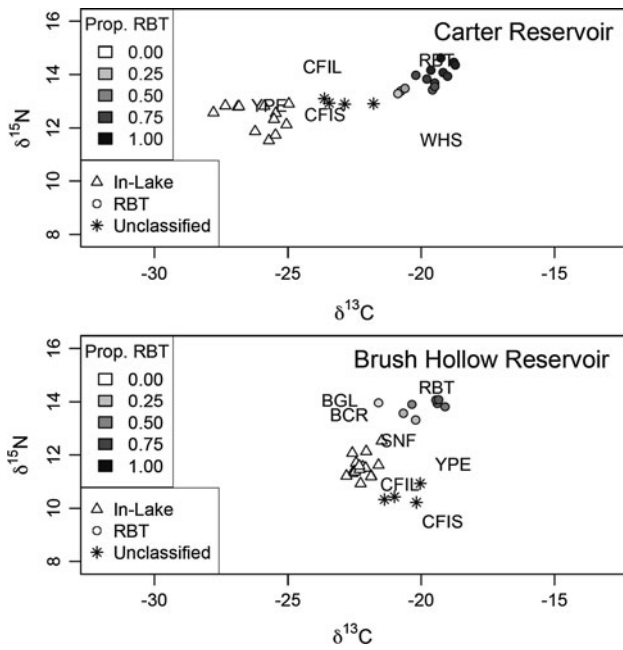


Fig. 2 Proportions of walleye diets consisting of RBT (Rainbow trout) based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of walleye and their prey, and cluster analysis results. The shading, in gray-scale, filling each point represents the proportion of RBT (Prop. RBT) in walleye diets, white = 0 % and black = 100 %. Prey item abbreviations are shown at their mean isotopic signatures (BCR, black crappie (*Pomoxis nigromaculatus*); BGL, bluegill sunfish (*Lepomis macrochirus*); CFIL, large crayfish, CFIS, small crayfish, RBT, rainbow trout, SNF, sunfish hybrids (*Lepomis* spp); WHS, white sucker (*Catostomus commersonii*); YPE, yellow perch (*Perca flavescens*)). Individuals categorized as “in-lake” and “RBT” consumers are represented with triangles and circles respectively. “Unclassified” individuals are represented by asterisks

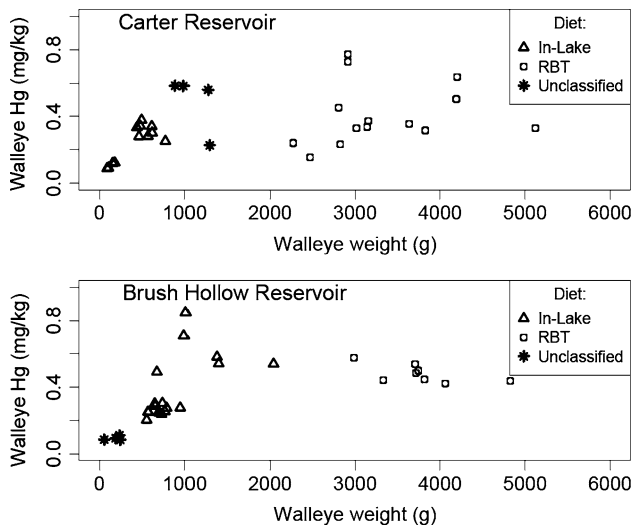


Fig. 3 Individual walleye Hg concentrations as a function of weight. Individuals categorized as “in-lake” and “RBT” consumers are represented with triangles and circles respectively. “Unclassified” individuals are represented by asterisks

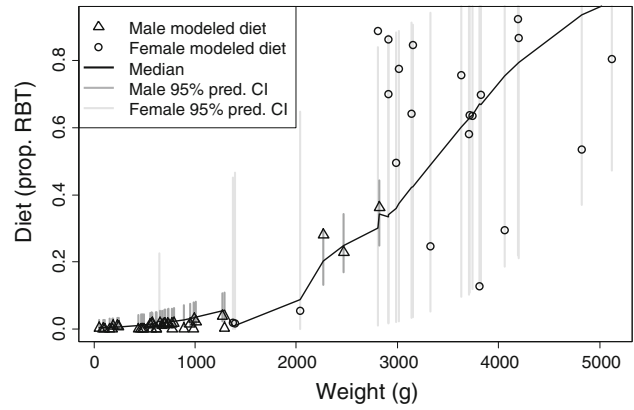


Fig. 4 Posterior predictive distribution from the beta regression of walleye diet. Diet is expressed as a proportion of RBT, rainbow trout or p_i , as a function of fish sex and weight. Beta regression posterior means and 95 % credible intervals were β_0 (intercept) = -1.26 (-1.33, -1.18), β_1 (weight) = 1.12 (1.00, 1.22), α_1 (male) 4.84 (4.27, 5.30), and $\alpha_1 + \alpha_0$ (female) = 1.13 (0.62, 1.62) respectively. Note that the weight covariate was standardized by subtracting the mean and dividing by the standard deviation

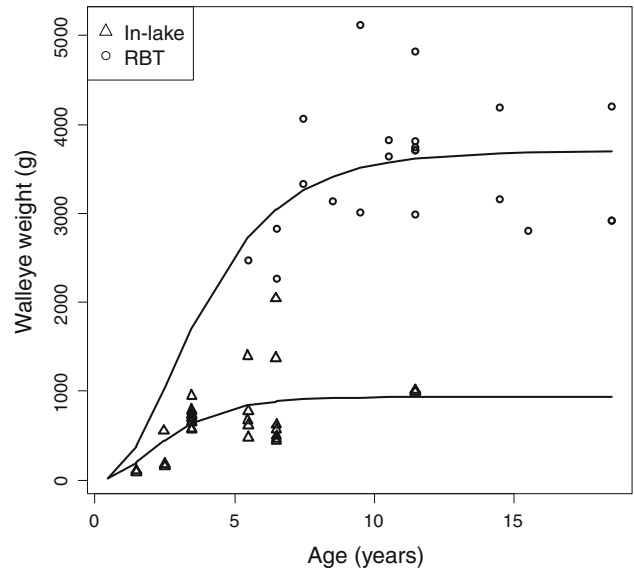


Fig. 5 Nonlinear model fits of von Bertalanffy growth functions for the two clusters of walleye; in-lake and RBT (rainbow trout) consumers represented by triangles and circles respectively

contrast, consumption of in-lake prey items resulted in walleye with relatively poor growth and high Hg concentrations, which were not the largest fish within the study systems. It is important to note that only a portion of the walleye in the study populations were consuming RBT, while others focused on in-lake prey.

Of the 2 billion fish stocked globally every year, by weight, over 60 % of those are RBT (Halverson 2010). Further, RBT represent a single hatchery-reared species and many other species are reared for stocking throughout the world (de Jong et al. 2004; Povz and Sumer 2005;

Rahel 2000) on the order of 18 million kg of fish annually (Halverson 2010). Eby et al. 2006 discussed the effects of stocking in freshwater systems including alterations to nutrient fluxes, food web structure, community composition, competition, and predator–prey interactions. Similarly, our study showed sport fish Hg concentrations can be lower than expected when hatchery subsidies in the form of relatively high quality, low Hg forage contribute to freshwater food webs.

Globally, humans harvest approximately 100 million metric tons of marine organisms each year, and the majority of these are distributed to freshwater and terrestrial systems by some method (e.g., as feed for fish stocked into freshwater systems, direct consumption and digestion by humans, or use in feed for agricultural animals; FAO 2009). Thus, a potentially large source of external energy and contaminants to freshwater and terrestrial systems is in the form of marine-derived subsidies. As such, these subsidies can affect contaminant bioaccumulation in recipient systems, and create linkages in the mercury cycle among marine, terrestrial and freshwater ecosystems at a global scale.

Growth and diet composition (energy and Hg content) are important factors influencing Hg concentrations, specifically in walleye (Harris and Bodaly 1998; Simoneau et al. 2005; Swanson et al. 2003) and our study is consistent with those findings. More specifically, our results corroborate those of Lepak et al. 2012 where sport fish feeding on stocked RBT experienced biomass dilution of Hg resulting from increased growth. We observed that walleye consuming primarily RBT with high energy density and low Hg concentrations were relatively large and these walleye had Hg concentrations lower than expected given their size. Importantly, the differences we observed in walleye diet, growth and Hg concentrations were associated with walleye sex, with females focusing more on stocked RBT as an energy source than males. Thus, knowledge of fish sex and size together could prove to be a valuable predictor of walleye Hg concentrations in systems with characteristics similar to the study reservoirs and would provide more informed and appropriate fish consumption advice for the public than current length-based advisories.

Sexual dimorphism in walleye has been documented in the past and has been linked specifically to differences in Hg concentrations. Henderson et al. 2003 noted that males grew more slowly and had higher Hg concentrations than females and attributed this largely to increased activity associated with spawning costs (competition) in male walleye. McClain et al. 2006 observed similar patterns in male and female walleye growth and Hg concentrations and alluded to Henderson et al. 2003 to explain these findings. Rennie et al. 2008 suggested that differences in male and female walleye growth and Hg concentrations

were likely attributable to “laziness”, suggesting that male walleye foraging was greatly reduced at the onset of maturity presumably to avoid predation as posited by Roff 1983, though the authors did not discount the importance of the supposition by Henderson et al. 2003. Our results indicate that another mechanism may be influencing walleye sexual dimorphism and Hg concentrations. We observed that male and female walleye prey selection was disparate, with males focusing almost exclusively on smaller, resident fish and invertebrates (relatively low quality) while females transitioned to larger prey (stocked RBT, relatively high quality) as they became larger. Differences in diet had a significant influence on walleye growth and Hg concentrations and could be influencing sexual dimorphism in walleye and other fish populations where both high quality (e.g., pelagic salmonines or coregonids) and low quality (e.g., littoral invertebrates) forage are available. In some systems, male walleye selectively consume invertebrates and grow poorly relative to others, which support our supposition (Paradis et al. 2006). Though we do not discount the potential importance of walleye spawning and predator avoidance behaviours influencing sexual dimorphism, we emphasize that differences in prey energy densities (nearly two-fold in cases) and digestibility could produce the observed gender-based differences in walleye growth, subsequently contributing to differences in walleye Hg concentrations.

The results presented here suggest that hatchery subsidies can influence sport fish growth in freshwater systems and this is likely occurring in highly managed systems throughout the world. In addition, hatchery subsidies may influence Hg concentrations in freshwater sport fish depending on the Hg concentrations of the subsidies themselves. We hypothesize that the use of hatchery fish (particularly catchable-sized salmonids) as prey to support piscivore populations and alter Hg concentrations would be cost prohibitive and potentially ecologically harmful, especially in large systems (Iwama 1991; Johnson and Martinez 2000; Knapp et al. 2001). If enough hatchery subsidies were provided to satisfy piscivorous sport fish consumptive demand, stocking prey would likely enhance piscivore reproduction and growth and increase their subsequent demand for future subsidies. Thus, although stocking is an appealing idea for controlling sport fish Hg concentrations, it may only be feasible in unusual circumstances (e.g., in stocked, sterile predator populations or those that have some other reproductive constraint) and other management options may be more practical, especially when considering costs at large scales.

Perhaps a more effective strategy to control Hg bioaccumulation is to manage fisheries with the goal of shifting sport fish diets to relatively high energy and low Hg prey items when available naturally. Management actions aimed

at increasing the abundance and availability of beneficial prey species could be used to decrease Hg concentrations in the predators that consume them. It is important to note that this is not always possible and even when high energy, low Hg prey are available, some sport fish (e.g., male walleye in this case) may behave differently than others in the population, feeding on prey that result in relatively poor growth and high Hg concentrations. Thus, under some conditions it may be advantageous to human health to manage fisheries with non-piscivorous species (e.g., rainbow trout or kokanee salmon (*Oncorhynchus nerka*)) as apex predators to reduce human exposure to contaminants. Similarly, fast growing salmonids have been suggested as desirable species to stock as apex predators in the Great Lakes (USA) to reduce contaminant exposure in anglers (Stow et al. 1995). Alternatively, if Hg concentrations in some species of sport fish cannot be reduced, it will be necessary to continue managing fisheries as they are today, in the presence of contaminated predators. As a result, further research and efforts to effectively inform anglers of the risks associated with harvesting and consuming particular species are necessary.

Characterizing food webs in highly managed reservoirs provided pertinent information about Hg bioaccumulation in these relatively understudied systems. We observed that hatchery subsidies may be influencing sport fish diet, growth and Hg concentrations in some situations. We also observed that, within systems, external subsidies may be affecting growth and Hg concentrations disparately in individual sport fish of the same species. Thus, caution must be exercised by policy makers to protect human health when variability in sport fish Hg concentration is atypical (i.e., the largest individuals in the system do not have the highest Hg concentrations) because of artificial subsidies. Fish consumption advisories often mimic maximum size limits of harvest regulations: a length threshold is set, below which harvest (and consumption) is acceptable (or less harmful). In subsidized fisheries, smaller piscivores may be more contaminated than expected relative to larger individuals, and consumption advice to the public should reflect this. It is important to note that our findings were related to systems where “large” fish (i.e., intended for immediate capture by anglers) were being stocked. Thus, these types of systems may show patterns of Hg bioaccumulation in fish that are dissimilar from others where larger fish tend to have higher concentrations of Hg. In areas where smaller fish are being stocked with the intention of allowing them to grow on in-lake prey sources for later capture by anglers, different patterns may arise. Thus, we suggest that more focused research be conducted on systems experiencing external subsidies in the form of stocked fish with differing management approaches.

The influence of external subsidies on terrestrial and aquatic food webs (including humans as apex predators) is pervasive, and their impacts on food webs must be considered at multiple levels (i.e., primary, secondary, tertiary, etc.) especially in the context of nutrient and contaminant cycling. As aquacultural fish production continues to increase, and per capita harvest of large fish species continues to decline (FAO 2009), our primary, secondary and tertiary reliance on energy sources in the form of fish meal may become increasingly important. Thus, understanding the impacts of fish meal at various levels as a source of energy and contaminants to terrestrial and aquatic systems is imperative.

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Ethical standards The experiment described in this manuscript complies with the current laws of the country in which it was performed.

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